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NEKTON USE OF MACROPHYTE PATCHES FOLLOWING MORTALITY OF TURTLEGRASS, *THALASSIA TESTUDINUM*, IN SHALLOW WATERS OF FLORIDA BAY (FLORIDA, USA)

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ABSTRACT

Widespread seagrass mortality in western Florida Bay has led to increased habitat heterogeneity: once-dominant *Thalassia testudinum* beds have become punctuated by mud, algae, and *Halodule wrightii* patches. We tested the hypothesis that increased habitat heterogeneity leads to increased secondary production and diversity. Nekton densities in shallow (depths <1 m) *Thalassia* meadows and in mud, algae, and *Halodule* patches were compared 12 times over 3 yrs using a quantitative 2.6 m² drop trap. Mean densities of fishes and decapods were usually significantly higher in *Thalassia* beds than in *Halodule*, algae, and mud patches. The reverse was true for species diversity and richness, which were usually significantly lower in *Thalassia* beds than in one or more patch types. Macrofaunal densities and species richness and diversity were usually not affected by site (two areas 15 km apart) or time (day vs. night). Six species comprised 84-99% of all organisms in each floral type. Mean densities of *Lucania parva*, *Opsanus beta*, and *Thor floridanus* were almost always significantly higher in *Thalassia* beds than in *Halodule*, algae or mud patches. The opposite was true for mean densities of *Floridichthys carpio*, which were usually significantly lower in *Thalassia* than elsewhere. Mean densities of *Penaeus duorarum* were irregularly related to plant type, and those of *Gobiosoma robustum* were never related to plant type. Time of collection did not affect densities of any dominant species, but mean densities of *Thor* and *Floridichthys* were significantly higher on Ninemile Bank than on Sandy Key Bank. Lower nekton standing crops and increased species richness and diversity at the local scale may lead to system-wide faunal changes. However, fisheries seem not to have been affected by seagrass mortality and associated changes in habitat heterogeneity and the forage base.

Substantial portions of the seagrass ecosystem of Florida Bay (Florida, USA) have experienced a major floral change since 1987: widespread mortality of turtlegrass *Thalassia testudinum* (Robblee et al., 1991) has led to colonization of denuded mud patches by various algal genera and by shoalgrass *Halodule wrightii* (Thayer et al., 1994). At least 4000 ha of *Thalassia* have been denuded and 23,000 ha have been impacted to a lesser degree since 1987 (>16% of the total seagrass habitat; Robblee et al., 1991). These mortality events, coupled with related phenomena such as increased turbidity due to sediment resuspension and to algal blooms (Durako et al., 1995), could affect system productivity by altering distributions and abundances of fishery and forage organisms (Thayer et al., 1994).

Prior to 1987, seagrass meadows covered 1660 km² of Florida Bay and were dominated by *Thalassia*, which occurred at 95% of 108 stations and formed 82% of the macrophyte standing crop, excluding drift algae (Zieman et al., 1989). *Halodule* and manatee grass *Syringodium filiforme* occurred less frequently (48% and 13% occurrence, respectively), and each comprised about 5% of the standing crop. Attached algae such as *Batophora oerstedii*, *Acetabularia crenulata*, and *Penicillus* spp. occurred at 50% of the stations and

formed 8% of the biomass. Non-vegetated mud was recorded infrequently (<4% of the stations; Zieman et al., 1989). Bay-wide assessments of floral composition following the 1987 start of *Thalassia* mortality were not begun until 1995 (Durako et al., 1995), aside from early observations by Robblee et al. (1991).

Even though system-wide changes were not well documented, Thayer et al. (1994) examined local dynamics of macrophyte patches during 1990-1992 mortality events in Johnson Key and Rabbit Key Basins, two areas in western Florida Bay that were among the earliest to be impacted. Denuded mud patches (1 to 10 m²) caused by *Thalassia* mortality were relatively ephemeral, appearing and disappearing in 2 to 4 mo as mud was colonized first by algae (*Batophora oerstedii*, *Halimeda* spp., and *Penicillus* spp.) and then by *Halodule* (Robblee et al., 1991; Thayer et al., 1994). Once seagrasses began to colonize, *Halodule* dominated these small patches in 3-12 mo but was replaced by *Thalassia* in 12-14 mo. Repeated floral mortality was noted following colonization of specific patches, in part attributable to increased turbidity that reduced light penetration (Thayer et al., 1994).

Such changes in floral community structure are expected to alter macrofaunal communities. Increased habitat heterogeneity is hypothesized to increase secondary production and diversity (Connell, 1978; Sousa, 1979a, b), and there is evidence for these responses in Florida Bay from comparisons of fish communities inhabiting mixed versus monospecific seagrass beds (Rutherford et al., 1989a; Thayer and Chester, 1989; Chester and Thayer, 1990). System-wide assessments of the effects of *Thalassia* mortality on macrofauna are currently in progress (Colvocoresses and McMichael, 1995), since the seagrass ecosystems of south Florida support a wide variety of commercial and recreational fisheries (Tilmant, 1989; Bohnsack et al., 1994). Ex-vessel value of these fisheries for Dade and Monroe Counties in southernmost Florida exceeded \$40 million in 1996 (S. Brown, Florida Department of Environmental Protection, pers. comm.). Florida Bay is also a nursery area for larval and juvenile stages of many fishery organisms and supports a diverse community of small forage fishes and decapods (Costello et al., 1986; Sogard et al., 1987; Holmquist et al., 1989a,b; Powell et al., 1989; Rutherford et al., 1989a,b,c; Thayer and Chester, 1989; Chester and Thayer, 1990). In this paper we report on densities of fishes and decapods inhabiting *Thalassia* and local macrophyte patches formed by *Thalassia* mortality in shallow waters of western Florida Bay.

MATERIALS AND METHODS

SAMPLING DESIGN. — Florida Bay is bordered on the north, east and south by mainland Florida and the Florida Keys (Monroe and Dade Counties), and it is open to the Gulf of Mexico on the west (Fig. 1). Shallow banks divide the 2200 km² bay into a series of deeper basins. Sampling sites were located on *Thalassia*-dominated banks surrounding Johnson Key Basin (25° 03' N, 80° 55' W) and on eastern Ninemile Bank adjoining Rabbit Key Basin (24° 48' N, 80° 51' W; Fig. 1). Sampling near Johnson Key was conducted on eastern Sandy Key Bank during 1990-1991 but was moved 4 km northeast to western Dildo Key Bank in 1992-1993 due to extensive seagrass mortality and continuously increasing water turbidity (Thayer et al., 1994; pers. obs.).

Fish and decapod densities in *Thalassia* meadows and in mud, algae, and *Halodule* patches on shallow bank-tops (depths <1 m) were compared using a quantitative 2.6 m² drop trap (Zimmerman et al., 1984). Study sites were areas where all four habitats existed within a 2-km radius at least 2 km from the nearest mangrove key. We compared daylight (08:00-18:00) fish and decapod communities in each of the four floral types on Sandy Key Bank at 6 to 8 wk intervals during July,

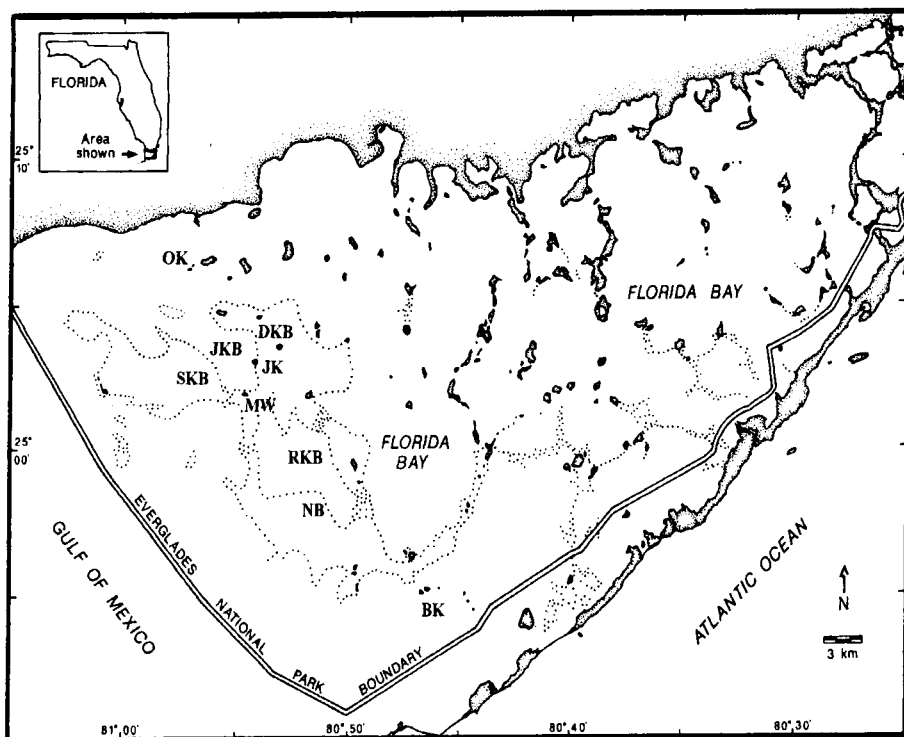


Figure 1. Location of sampling sites in Florida Bay. BK = Buchanan Key, DKB = Dildo Key Bank, JK = Johnson Key, JKB = Johnson Key Basin, MW = Man of War Key, NB = Ninemile Bank, OK = Oyster Key, RKB = Rabbit Key Basin, SKB = Sandy Key Bank.

August, and October 1990 and April 1991 (sampling dates 1-4, designated Year 1). We then compared daylight samples at Sandy Key Bank and 15 km away at Ninemile Bank on four occasions (June, July, August, and October 1991; sampling dates 5-8, designated Year 2) to determine whether trends in faunal abundance were site-specific. Finally, we compared daylight (08:00-18:00) and nocturnal (21:00-05:00) samples from Dildo Key Bank on four occasions (May, June, and August 1992 and April 1993; sampling dates 9-12, designated Year 3) to determine whether time of day affected faunal densities in any of the floral types. Collections were made primarily during the wet season (May - October) when faunal densities were expected to be highest (Thayer et al., 1987; Holmquist et al., 1989a,b).

SAMPLING METHODS. — Drop trap samples were taken haphazardly, based on visual location of patch types and distances of ≥ 10 m between samples (markers were placed nearby during daylight hours for later nocturnal sampling). *Thalassia* samples were collected at least 10 m from mud, algae, or *Halodule* patches. Sites were not marked for repetitive sampling and were not intentionally re-sampled in subsequent months. Species composition of algal patches was not controlled, but patches were most frequently monospecific stands of *Penicillus capitatus* or *Halimeda incrassata* and less frequently *Udotea flabellum* or *Caulerpa ashmeadii* on Sandy Key Bank and primarily *Batophora oerstedii* on Dildo Key Bank and Ninemile Bank (identified using Woelkerling, 1976). All four floral types occasionally harbored *Acetabularia crenulata* and mixed drift algae. All samples during a given month were collected within 4 d.

Six replicate drop trap samples were collected in each floral type each month to estimate faunal abundance, following methods of Zimmerman et al. (1984). Minimum and maximum water depths, salinity and temperature were measured within the drop trap using a meter stick, a temperature-

compensated refractometer, and a stick thermometer. Enclosed organisms were removed first by sweeping the area with dip nets, then by pumping all water out of the trap through a 3-mm mesh net and picking all visible organisms off the bottom. Organisms were preserved in 10% formalin. Sampling and data entry at night were conducted using a single flashlight (or no lights, if moonlight was sufficient), and lanterns were suspended over the drop trap to aid removal of organisms. Common names for decapods and fishes follow Williams et al. (1989) and Robins et al. (1991). Some specimens could not be identified with certainty beyond family or genus due to small size or to damage during collection or preservation. Organisms in each sample were then grouped into major taxa (fishes, shrimps, crabs), blotted, and weighed to estimate biomass. We deployed a single data logger (Data Sonde 3, Hydrolab Corp., Austin, Texas) near the Sandy Key Bank or Dildo Key Bank sampling areas for remote hourly collection of dissolved oxygen concentrations during 1991-93.

Drop trap efficiency in mixed seagrasses was reported by Sheridan (1992) to be 82% recapture of marked fishes and decapods. Several daylight mark-recapture experiments were conducted in each floral patch type during this study by releasing fin- or uropod-clipped organisms into a deployed drop trap, then recapturing after ≥ 30 min by methods described above. Commonly occurring organisms comprising 13 fish species and 4 decapod species (218 individuals total) were tested. Recaptures by habitat were: *Thalassia*, 79%; mud, 100%; algae, 93%; *Halodule*, 83%; and overall, 88%. These values were primarily influenced by our inability to recapture gulf toadfish *Opsanus beta* which often remained burrowed for 5-10 min after all water was removed from the drop trap.

We made quantitative estimates of above-ground plant biomass within each drop trap using a modification of Fonseca et al. (1990). Densities of algae with widely spaced holdfasts or prostrate thalli (*Halimeda*, *Penicillus*, *Udotea*, and *Caulerpa*) were often low enough to count all plants within the drop trap. At higher densities, estimates of numerical abundance were made from the combined count of plants within three 0.0683 m² or 0.0625 m² quadrats placed haphazardly within the drop trap. Representative specimens of these algae at each site were preserved for later determination of biomass. Densities of *Batophora*, *Halodule*, and *Thalassia* were estimated from the preserved contents of one 10-cm diameter (0.0079 m²) core taken within the drop trap. Plant material was later rinsed in 10% phosphoric acid to remove carbonates, then dried at 90° C to a constant weight. Above-ground biomass per m² was calculated from counts per unit area and dry weights of solitary algae or from dry weights of *Batophora* or seagrass shoots per core. Shoot densities were estimated in a similar manner, except for *Batophora* which often broke apart during preservation.

DATA ANALYSIS. — For Year 1, we employed two-way analysis of variance (ANOVA) to test effects of Plant type and Month on faunal densities. For Year 2, we employed split-plot ANOVA to test effects of Plant, Site (Dildo Key Bank vs. Ninemile Bank), and Month on faunal densities, using the model:

$$Y = \text{Plant} + \text{Site} + \text{Site} \times \text{Plant} + \text{Month} + \text{Month} \times \text{Plant} + \text{error}.$$

A similar model was used to assess Time (day or night) in place of Site for Year 3. In split-plot ANOVA, the main effects of Site or Time and Plant are tested over the whole-plot error (Site x Plant or Time x Plant interactions), whereas Month and Month x Plant are tested over the sub-plot error (Snedecor and Cochran, 1967). In a split-plot design, whole-plot error typically is larger than sub-plot error and, consequently, F tests of main effects are more conservative than in a three-way randomized design (Snedecor and Cochran, 1967). Type III sums of squares were used to derive mean squares for F tests, since interaction terms preceded main effects in the split-plot models (SAS Institute Inc., 1985). When significant main effects were indicated by ANOVA, Ryan's Q test ($\alpha = 0.05$) was used to detect differences in treatment means (Day and Quinn, 1989). Balanced cell sizes were maintained except for loss of one daylight faunal sample from algae in June 1992 and one nocturnal faunal sample each from *Thalassia* and algae in April 1993. We tested for differences in the following: total fishes, total decapods, six recurring abundant species (defined as species with counts averaging ≥ 1 individual m⁻² in any habitat for 3 or 4 mo in each year), species richness

Table 1. Mean above-ground floral shoot density, biomass, and seagrass leaf length on Florida Bay seagrass banks. N = 6 per habitat per month, except n = 18 for leaf length. Algae listed in parentheses in decreasing frequency of occurrence as B = *Batophora*, C = *Caulerpa*, H = *Halimeda*, P = *Penicillus*, U = *Udotea*. * = not measured

Site	Year	Month	Shoots m ⁻²			Dry weight (g) m ⁻²			Leaf length (mm)	
			Algae	<i>Halodule</i>	<i>Thalassia</i>	Algae	<i>Halodule</i>	<i>Thalassia</i>	<i>Halodule</i>	<i>Thalassia</i>
Sandy Key	1990	Jul	113 (P)	2609	976	80.48	6.00	79.33	115	220
Bank		Aug	68 (PHU)	1824	912	25.38	4.02	58.44	115	226
		Oct	62 (PC)	3118	1294	6.83	9.17	63.05	132	222
	1991	Apr	59 (H)	2354	1146	59.66	5.59	61.88	145	176
		Jun	62 (PH)	1846	827	49.26	4.02	78.91	113	240
		Jul	109 (P)	2227	891	32.41	5.72	88.14	119	289
		Aug	87 (P)	1761	721	28.04	5.93	64.27	122	275
		Oct	30 (PH)	1740	573	20.82	2.99	50.86	94	244
		Jun	* (B)	1103	700	96.53	3.52	56.48	105	169
Bank		Jul	* (B)	1867	1061	39.28	6.10	41.75	127	133
		Aug	* (B)	2524	573	36.82	6.29	39.24	125	133
		Oct	* (B)	1909	976	58.98	6.04	51.70	119	175
Dildo Key	1992	May	* (B)	2800	848	28.94	8.04	99.88	142	224
Bank		Jun	* (B)	806	1018	6.04	2.79	84.12	87	191
		Aug	* (B)	2524	827	18.53	5.08	80.09	118	219
	1993	Apr	* (B)	1476	849	35.50	2.78	40.42	71	131

[(S-1)/log N, where S = number of species and N = number of individuals], and species diversity (Shannon's index $H' = \sum p_i \log p_i$, where p_i = proportion of species i in the sample; Pielou, 1969).

Sample size was determined from a series of 10 faunal and floral samples collected with the same gear during September 1988 from mixed seagrasses in Rookery Bay, Florida, 170 km northwest of Florida Bay (Sheridan, 1992). We subjected this data set to a power analysis, after log (x+1) transformation of faunal densities (Sokal and Rohlf, 1981). With six samples from each habitat, we could detect a 100% difference in log-transformed means with $\alpha = 0.10$ and $1 - \beta = \text{power} = 0.80$ for nine of 10 dominant fishes and decapods, total fishes, total decapods, and seagrass biomass. We analyzed a set of 15 daylight faunal samples from *Thalassia* after commencement of sampling to check the validity of the design. This analysis indicated that with six samples per floral type we could detect a 100% difference in log-transformed means with $\alpha = 0.10$ and $\text{power} = 0.75$ for six of eight dominant species, total fishes, and total decapods. Thus, our sampling design had relatively high power with respect to these variables. A much larger set of samples (14 for decapods, 35 for fishes) would have been required to maintain similar power to detect differences in fish and decapod biomasses, so biomass data are excluded from this report.

Distributions of error terms for each abundant species and major group usually violated assumptions of normality, as indicated by the Shapiro-Wilk test statistic (Shapiro and Wilk, 1965). Positive relationships between means and variances were detected, so log (x+1) transformation was used to successfully achieve homogeneity of variances. Distributions of error terms for species richness and diversity exhibited normality. All analyses were conducted using SAS personal computer software programs (SAS Institute Inc., 1985).

RESULTS

WATER COLUMN CHARACTERISTICS. — Western Florida Bay seagrass bank-tops were often hypersaline, averaging over 35‰ in 9 of 12 sampling months. Average salinities ranged from 46‰ in June 1991 to 30‰ in June 1992. Banks were prone to high temperatures (maximum mean of 33.6 °C over all samples in June 1991) resulting from a combination

Table 2. Mean density (number m⁻²) of fishes and decapods captured from *Thalassia testudinum* (Thal), mud, algae, and *Halodule wrightii* (Halo) on Sandy Key, Ninemile, and Dildo Key Banks in western Florida Bay between July 1990 and April 1993, using a 2.6 m² drop trap. N = 120 for mud and *Halodule*, 119 for *Thalassia*, and 118 for algae. Identification to family or genus only indicates juveniles or damaged specimens.

Fishes	Macrophyte type				Decapods	Macrophyte type			
	Thal	Mud	Algae	Halo		Thal	Mud	Algae	Halo
<i>Lucania parva</i>	50.7	5.0	5.7	26.4	<i>Thor floridanus</i>	431.1	20.8	24.1	139.9
<i>Gobiosoma robustum</i>	8.1	4.8	6.2	6.4	<i>Hippolyte zostericola</i>	11.3	1.2	1.0	5.9
<i>Opsanus beta</i>	7.4	0.6	1.1	2.9	<i>Penaeus duorarum</i>	4.4	5.8	6.5	9.5
<i>Floridichthys carpio</i>	2.9	8.7	9.2	13.8	<i>Pagurus maclaughlinae</i>	0.2	1.5	1.1	1.2
<i>Lutjanus griseus</i>	2.5	0.1	0.5	0.5	<i>Alpheus heterochaelis</i>	1.2	<0.1	0.2	0.6
<i>Microgobius gulosus</i>	0.2	1.6	1.0	0.9	<i>Periclimenes americanus</i>	0.7	0.1	0.3	1.1
<i>Syngnathus scovelli</i>	0.6	0.4	0.4	1.0	<i>Palaemonetes pugio</i>	0.8	0.1	0.1	0.1
<i>Anarchopterus criniger</i>	0.6	0.1	0.4	0.4	<i>Libinia dubia</i>	0.7	0.2	0.4	0.5
<i>Lagodon rhomboides</i>	0.4	<0.1	<0.1	0.2	<i>Neopanope packardii</i>	0.6	<0.1	0.1	0.3
<i>Hippocampus zosterae</i>	0.4	0.1	0.1	0.3	<i>Palaemonetes intermedius</i>	0.2	<0.1	<0.1	<0.1
<i>Gobiosoma bosc</i>	0.2	<0.1	0.1	-	<i>Paguristes tortugae</i>	0.2	0.1	0.1	0.1
<i>Syngnathus floridanus</i>	0.1	<0.1	0.1	0.1	<i>Dyspanopeus sayi</i>	0.1	<0.1	-	<0.1
<i>Eucinostomus gula</i>	0.1	0.3	0.4	0.6	Xanthidae	0.1	<0.1	<0.1	<0.1
<i>Strongylura notata</i>	0.1	<0.1	<0.1	0.1	<i>Tozeuma carolinense</i>	0.1	<0.1	<0.1	0.5
<i>Symphurus plagiusa</i>	0.1	0.6	0.6	0.4	<i>Dyspanopeus texana</i>	0.1	<0.1	<0.1	<0.1
<i>Myrophis punctatus</i>	<0.1	<0.1	-	-	<i>Palaemonetes</i> sp.	0.1	<0.1	<0.1	<0.1
<i>Chasmodes saburrae</i>	<0.1	<0.1	-	<0.1	<i>Neopanope</i> sp.	0.1	<0.1	<0.1	0.1
<i>Strongylura</i> sp.	<0.1	-	-	-	<i>Palaemon floridanus</i>	<0.1	-	<0.1	<0.1
<i>Synodus foetens</i>	<0.1	0.3	0.1	0.1	<i>Periclimenes longicaudatus</i>	<0.1	0.3	0.1	0.3
<i>Achirus lineatus</i>	<0.1	0.1	0.1	0.1	<i>Callinectes sapidus</i>	<0.1	<0.1	0.1	0.1
<i>Eucinostomus harengulus</i>	<0.1	<0.1	<0.1	<0.1	<i>Portunus gibbesii</i>	<0.1	0.3	0.1	0.1
<i>Syngnathus louisianae</i>	<0.1	-	<0.1	-	<i>Callinectes similis</i>	<0.1	0.1	0.1	0.1
<i>Orthopristis chrysoptera</i>	<0.1	-	-	0.1	<i>Alpheus normanni</i>	<0.1	<0.1	<0.1	<0.1
<i>Paralichthys albigutta</i>	<0.1	-	-	<0.1	<i>Processa hemphilli</i>	<0.1	<0.1	<0.1	0.1
<i>Cynoscion nebulosus</i>	<0.1	-	-	-	<i>Panopeus occidentalis</i>	<0.1	<0.1	-	-

Table 2. Continued.

Fishes	Macrophyte type					Macrophyte type				
	Thal	Mud	Algae	Halo	Decapods	Thal	Mud	Algae	Halo	
Gobiidae	-	0.2	-	-	<i>Callinectes ornatus</i>	< 0.1	-	< 0.1	-	-
<i>Atherinomorus stipes</i>	-	< 0.1	0.2	< 0.1	<i>Pinnixa</i> sp.	< 0.1	-	< 0.1	< 0.1	< 0.1
<i>Prionotus scitulus</i>	-	< 0.1	< 0.1	-	<i>Pinnixa sayana</i>	< 0.1	-	-	< 0.1	< 0.1
<i>Prionotus tribulus</i>	-	< 0.1	-	-	<i>Leander tenuicornis</i>	< 0.1	-	-	-	-
<i>Eucinostomus</i> sp.	-	< 0.1	-	< 0.1	<i>Panulirus argus</i>	< 0.1	-	-	-	-
<i>Eucinostomus lefrovi</i>	-	< 0.1	-	-	<i>Portunus</i> sp.	-	0.2	0.1	0.1	0.1
<i>Hippocampus erectus</i>	-	< 0.1	-	-	<i>Portunus ordwayi</i>	-	0.1	0.1	< 0.1	< 0.1
<i>Hyporhamphosus unifasciatus</i>	-	< 0.1	-	-	<i>Portunus sayi</i>	-	< 0.1	-	< 0.1	< 0.1
<i>Sardinella aurita</i>	-	< 0.1	-	< 0.1	<i>Portunus depressus</i>	-	< 0.1	-	< 0.1	< 0.1
Unidentified fish	-	< 0.1	-	-	Portunidae	-	0.1	< 0.1	< 0.1	< 0.1
<i>Gerres cinereus</i>	-	-	< 0.1	-	<i>Pagurus longicarpus</i>	-	< 0.1	< 0.1	-	-
<i>Strongylura marina</i>	-	-	< 0.1	-	<i>Pagurus</i> sp.	-	< 0.1	-	< 0.1	< 0.1
<i>Gobionellus boleosoma</i>	-	-	-	< 0.1	<i>Paguristes limonensis</i>	-	< 0.1	-	-	-
<i>Sphaeroides nephelus</i>	-	-	-	< 0.1	<i>Alpheus</i> sp.	-	< 0.1	-	-	-
<i>Anchoa</i> sp.	-	-	-	< 0.1	<i>Eurypanopeus depressus</i>	-	-	< 0.1	-	-
<i>Paraclinus marmoratus</i>	-	-	-	< 0.1	Diogenidae	-	-	-	< 0.1	< 0.1
<i>Sphyraena guachancho</i>	-	-	-	< 0.1	<i>Hippolyte curacaoensis</i>	-	-	-	< 0.1	< 0.1
					<i>Menippe mercenaria</i>	-	-	-	< 0.1	< 0.1
					<i>Portunus vocans</i>	-	-	-	< 0.1	< 0.1
					<i>Processa bermudensis</i>	-	-	-	< 0.1	< 0.1
All fishes	74.5	23.1	26.5	54.4	All decapods	452.0	31.0	34.5	160.8	

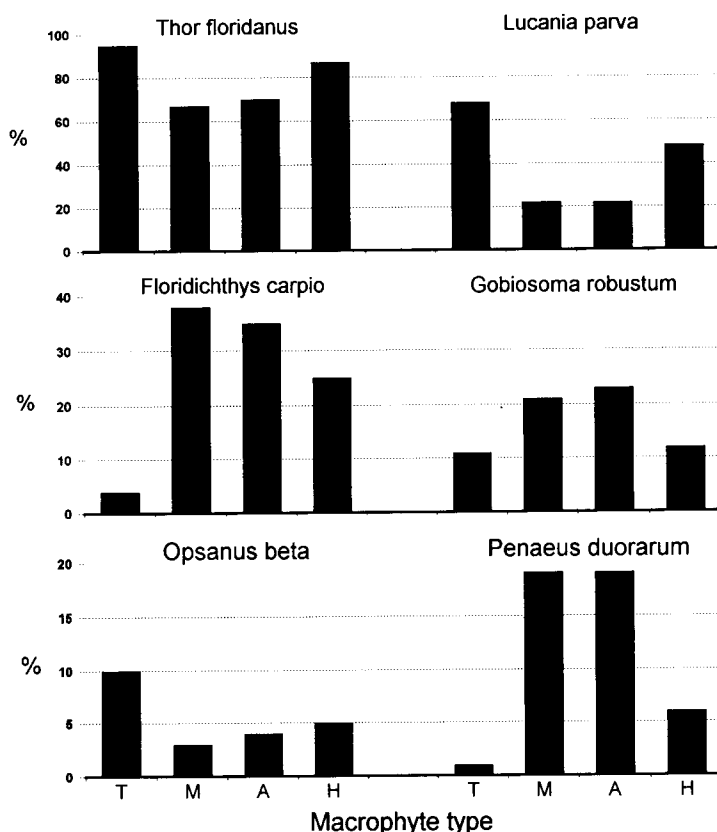


Figure 2. Dominant organisms (% of total fishes or decapods over all collections) by macrophyte type in western Florida Bay. T = *Thalassia*, M = mud, A = algae, H = *Halodule*.

of shallow waters that averaged 52 to 71 cm during our sampling periods, water retention by seagrass as tides recede from bank-tops, and bay-wide restricted circulation (Holmquist et al., 1989c; Powell and Schaffner, 1991). Dissolved oxygen fluctuated diurnally, with peaks usually near 17:00 and lows at 05:00. We recorded hypoxic water (<2 ppm) during October 1991 and August 1992. Hypoxia was most severe in October 1991: for four consecutive days, dissolved oxygen levels declined below 2 ppm at 02:00, reached 0.2 ppm, and only increased above 2 ppm after 08:00. Effects of nocturnal hypoxia on faunal abundance remain unknown, since day versus night samples during hypoxic events were only collected in August 1992 and produced no discernable faunal differences (discussed below).

FLORAL CHARACTERISTICS. — The floral patches found on seagrass bank-tops represented distinct successional environments (mud > algae > *Halodule* > *Thalassia*; Thayer et al., 1994). Two types of algal patch were found: structurally simple patches of “solitary” plants with low shoot densities such as *Caulerpa*, *Halimeda*, *Udotea* or *Penicillus*, and structurally complex aggregates of *Batophora* that often covered the bottom. Solitary plants dominated Sandy Key Bank in 1990 and 1991, whereas *Batophora* dominated

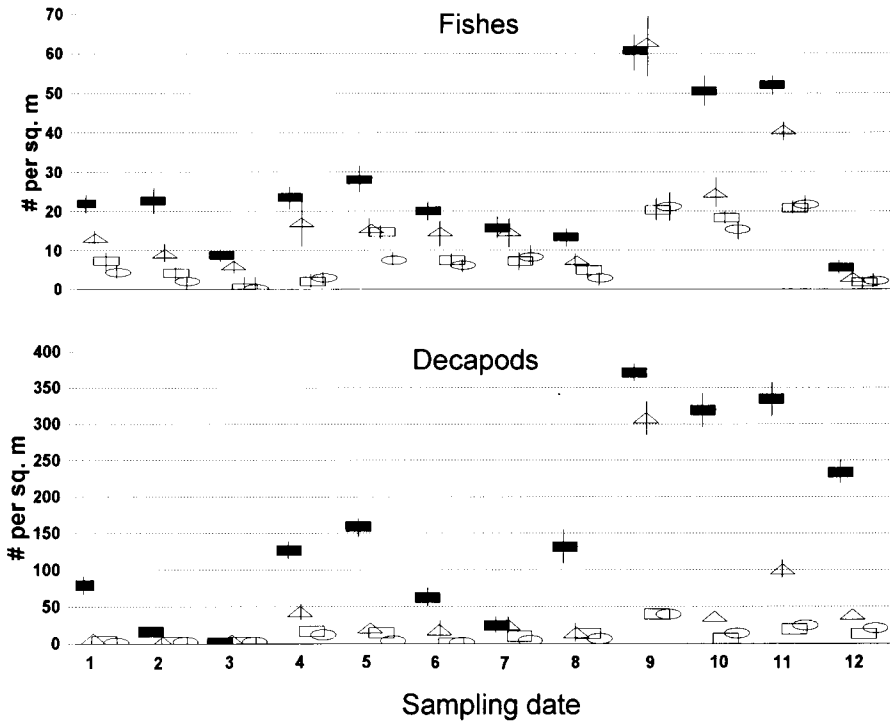


Figure 3. Mean densities of fishes and decapods by sampling date and macrophyte type. Closed box = *Thalassia*, open triangle = *Halodule*, open box = algae, open oval = mud. Vertical bar = ± 1 SE (if not visible, SE bar is smaller than symbol height).

algal patches on Dildo Key Bank and Ninemile Bank (Table 1). Algal biomass was typically highest in spring and early summer, as noted by Thayer et al. (1994).

Halodule represented a high shoot density, low biomass patch within the intermediate shoot density, high biomass *Thalassia* beds (Table 1). *Thalassia* shoot densities typically were lower than those of *Halodule* patches, but *Thalassia* leaves were up to twice as long and were an order of magnitude greater in biomass. *Halodule* densities, biomasses, and leaf lengths were similar among banks, whereas *Thalassia* was shorter and of lower biomass on Ninemile Bank than on Sandy Key or Dildo Key Banks (Table 1).

NEKTON ASSEMBLAGES. — A total of 37 fish species and 36 decapod species were identified over the 3-yr period (Table 2). Mean nekton densities were highest in *Thalassia*, intermediate in *Halodule*, and lowest in algae and mud. Most species were relatively rare, and only six species were considered regularly recurring fishes and decapods that comprised 84-99% of all organisms collected in each floral type. These species included rainwater killifish *Lucania parva*, goldspotted killifish *Floridichthys carpio*, code goby *Gobiosoma robustum*, gulf toadfish *Opsanus beta*, bryozoan shrimp *Thor floridanus*, and pink shrimp *Penaeus duorarum*. Other occasionally abundant species included gray snapper *Lutjanus griseus* (almost all collected in October 1991, particularly from *Thalassia*), clown goby *Microgobius gulosus* (mostly from Ninemile Bank in Year 2), gulf pipefish *Syngnathus scovelli* (each year during April - June), bigclaw snapping shrimp *Alpheus heterochaelis* (mostly from Dildo Key Bank in Year 3), and American grass shrimp

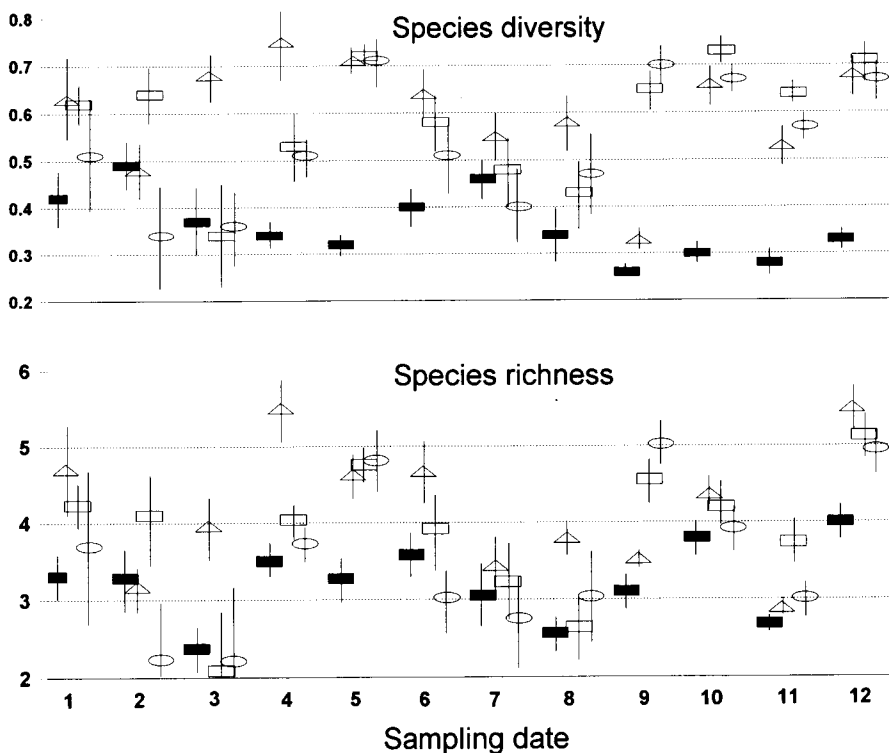


Figure 4. Mean species diversity and richness by sampling date and macrophyte type. Closed box = *Thalassia*, open triangle = *Halodule*, open box = algae, open oval = mud. Vertical bar = ± 1 SE (if not visible, SE bar is smaller than symbol height).

Periclimenes americanus and zostera shrimp *Hippolyte zostericola* (primarily collected in April 1991 and April 1993). The hermit crab *Pagurus maclaughlinae* was present in low numbers during all sampling dates. Although relatively large numbers of commercially and recreationally valuable pink shrimp and gray snapper were captured (3123 and 432 individuals, respectively; Table 2), only 40 individuals of other fishery species (blue crab *Callinectes sapidus*, gulf flounder *Paralichthys albigutta*, spotted seatrout *Cynoscion nebulosus*, and Florida stone crab *Menippe mercenaria*) were identified among more than 100,000 organisms collected.

The relative abundances of the six dominant species changed with macrophyte type (Fig. 2). Among fishes, *L. parva* dominated *Thalassia* beds and *Halodule* patches but was replaced by *F. carpio* and *G. robustum* in mud and algae patches. *O. beta* was most abundant in *Thalassia*. *T. floridanus* was the dominant decapod in all floral types, while *P. duorarum* was relatively more abundant in *Halodule*, mud, and algae patches than in *Thalassia*.

Macrofaunal densities and species richness and diversity in most cases were significantly different among plant types and months (Table 3). However, macrofaunal densities, species richness, and diversity were not significantly affected by site or time with one exception: mean decapod densities in Year 2 were three times greater on Ninemile Bank (51 m^{-2}) than on Sandy Key Bank (17 m^{-2}). Thus, only plant type and sampling

Table 3. Results of analyses of variance (ANOVA) comparing effects of plant type, site, time, and month on log (x+1) densities of fishes and decapods and on species richness and diversity. Two-way ANOVA was used for Year 1. Split-plot ANOVA was used for Years 2 and 3, wherein either the Site x Plant or the Time x Plant interaction was used as the whole plot error to test site, plant, and time main effects. * = $P < 0.05$, ** = $P < 0.01$.

Source of Variation	df	Fishes		Decapods		Species Richness		Species Diversity	
		MS	F	MS	F	MS	F	MS	F
Year 1									
Model	15	1.63	21.78**	2.19	22.09**	42.74	12.82**	0.11	3.32**
Plant	3	5.54	73.97**	3.52	35.55**	76.98	23.08**	0.27	8.30**
Month	3	2.05	27.39**	5.03	50.76**	114.01	34.18**	0.06	1.82
Month x Plant	9	0.19	2.51*	0.80	8.04**	7.58	2.27*	0.07	2.16*
Error	80	0.08		0.10		3.34		0.03	
Year 2									
Model	19	8.78	16.95**	18.84	10.91**	8.28	5.23**	0.25	7.84**
Site	1	51.57	8.64	110.32	142.08**	11.44	0.96	0.27	0.58
Plant	3	21.34	3.58	53.34	68.70**	9.28	0.78	0.51	1.11
Site x Plant	3	5.97	11.52**	0.78	0.45	11.92	7.53**	0.46	14.34**
Month	3	9.96	19.24**	14.47	8.38**	18.70	11.81**	0.26	7.95**
Month x Plant	9	0.39	0.74	4.66	2.70**	2.91	1.83	0.09	2.89**
Error	172	0.52		1.73		1.58		0.03	
Year 3									
Model	19	12.10	74.74**	21.76	35.06**	7.26	10.72**	0.29	25.68**
Time	1	0.17	0.32	22.52	8.40	3.45	6.05	0.04	1.97
Plant	3	13.36	24.74**	106.15	39.61**	9.95	17.45*	1.47	76.10**
Time x Plant	3	0.54	3.33*	2.68	4.32**	0.57	0.84	0.02	1.68
Month	3	60.91	376.14**	15.13	24.37**	25.27	37.34**	0.14	12.50**
Month x Plant	9	0.34	2.10*	2.23	3.59**	2.86	4.22**	0.07	6.31**
Error	169	0.16		0.62		0.68		0.01	

month were considered further. Mean densities of fishes and decapods were usually significantly higher ($P < 0.05$) in *Thalassia* beds than in *Halodule*, algae, and mud patches (Fig. 3). The reverse was true for species richness and diversity which were significantly lower in *Thalassia* beds than in one or more patch types (Fig. 4). Month was also a significant main effect each year, with the exception of diversity in Year 1. However, no particular month consistently exhibited significantly higher or lower density, richness, or diversity values. The month x plant interactions were also significant in Years 1 and 3 but not necessarily in Year 2. The nature of these interactions indicated that there was considerable variation among sampling dates within each year as to which floral types exhibited significant differences in faunal densities or community index values (Figs. 3 and 4).

Mean densities of four of the six dominant species differed significantly by plant type and month in most cases (Table 4). Significant ANOVA plant effects for *L. parva*, *O. beta*, and *T. floridanus* were almost always due to higher densities in *Thalassia* beds than in *Halodule*, algae, or mud patches (Figs. 5 and 6). The reverse was true for *F. carpio*, which had a significant plant effect related to mean densities that were usually lower in *Thalassia* than elsewhere (Fig. 6). Plant type had a significant effect on *P. duorarum* densities only in Year 1, and mean densities of *Gobiosoma* were never related to plant

Table 4. Results of analyses of variance (ANOVA P values only) comparing effects of plant type, site, time, and month on log (x+1) densities of recurring dominant fishes and decapods. Two-way ANOVA was used for Year 1. Split-plot ANOVA was used for Years 2 and 3, wherein the Site x Plant or the Time x Plant interaction was used as the whole plot error to test plant and site or time main effects.

Source of variation	<i>Lucania parva</i>	<i>Opsanus beta</i>	<i>Thor floridanus</i>	<i>Floridichthys carpio</i>	<i>Gobiosoma robustum</i>	<i>Penaeus duorarum</i>
<u>Year 1</u>						
Model	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Plant	< 0.001	< 0.001	< 0.001	< 0.001	0.090	0.002
Month	0.247	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Month x Plant	0.009	0.046	< 0.001	0.029	0.211	< 0.001
<u>Year 2</u>						
Model	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Site	0.622	0.101	0.017	0.022	0.055	0.505
Plant	0.034	< 0.001	0.054	0.046	0.295	0.285
Site x Plant	< 0.001	0.179	0.014	0.069	0.139	< 0.001
Month	< 0.001	< 0.001	< 0.001	0.005	< 0.001	< 0.001
Month x Plant	< 0.001	0.276	< 0.001	0.784	0.191	0.039
<u>Year 3</u>						
Model	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Time	0.822	0.085	0.078	0.592	0.628	0.261
Plant	0.001	0.001	0.013	0.039	0.295	0.424
Time x Plant	0.510	0.443	0.001	0.062	0.025	0.006
Month	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Month x Plant	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001

type (Table 4, Fig. 7). In most instances, month was also a significant main effect each year. However, no particular months consistently exhibited higher or lower faunal densities across the years. The month x plant interactions were almost always significant in Years 1-3 for all taxa except *Gobiosoma* (Table 4). The nature of these interactions indicated that there was considerable variation among sampling dates within each year as to which floral types exhibited significant differences in faunal densities. Time did not significantly affect densities of any of the six dominant species, but site had a significant effect on two dominants (Table 4). Mean densities of both *T. floridanus* and *F. carpio* in Year 2 were significantly higher on Ninemile Bank than on Sandy Key Bank (122 and 12 m⁻² versus 35 and 5 m⁻², respectively).

DISCUSSION

Shallow Florida Bay *Thalassia* beds sampled during 1990-93 continued to support the high faunal standing crops documented prior to the 1987 onset of seagrass mortality. Mean nekton densities in *Thalassia* during 1990-93 (75 fish m⁻² and 452 decapods m⁻²) exceeded those recorded during 1984-85 at Buchanan Key (12 fish m⁻², Sogard et al., 1987; 126 decapods m⁻², Holmquist et al., 1989a, b). Bank-top *Thalassia* in Florida Bay supported higher faunal densities than shallow seagrasses elsewhere in south Florida,

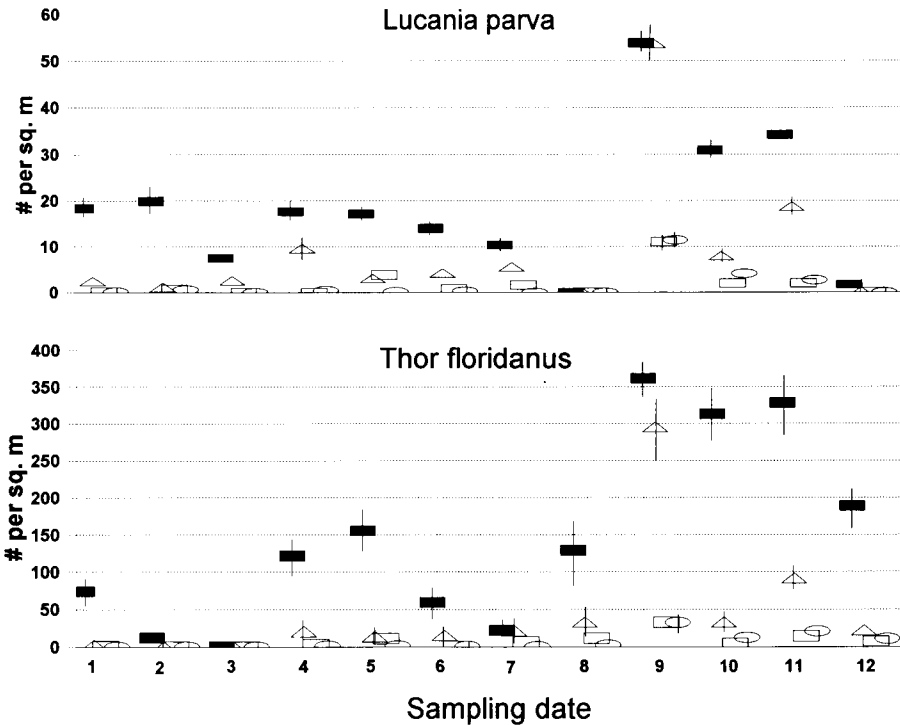


Figure 5. Mean densities of *Lucania parva* and *Thor floridanus* by sampling date and macrophyte type. Closed box = *Thalassia*, open triangle = *Halodule*, open box = algae, open oval = mud. Vertical bar = ± 1 SE (if not visible, SE bar is smaller than symbol height).

such as in Rookery Bay (6 fish m^{-2} and 83 decapods m^{-2} ; Sheridan, 1992) or Indian River Lagoon (66 fish m^{-2} , Snodgrass, 1992; 90 decapods m^{-2} , Gore et al., 1981).

Heterogeneous seagrass beds (encompassing patchy and bare areas) are hypothesized to provide more favorable foraging areas for small organisms since refuge lies adjacent to open feeding areas; thus, seagrass beds with more "edge" or ecotone per unit area should support a higher density of mobile foraging species than homogeneous seagrasses (Orth et al., 1984). Prior research in Florida Bay seemed to support this hypothesis, in that fish density and diversity were higher in heterogeneous seagrass habitats than in monospecific beds (Rutherford et al., 1989a; Thayer and Chester, 1989; Chester and Thayer, 1990). However, non-vegetated mud or sand habitats typically exhibit significantly lower faunal densities than do adjacent seagrasses (Summerson and Peterson, 1984; Fonseca et al., 1990; Thomas et al., 1990; Williams et al., 1990; Sogard and Able, 1991; Humphries et al., 1992; Connolly, 1994). Our data indicate this is often true for algal and *Halodule* patches as well. In western Florida Bay, mud patches were characterized by low faunal densities averaging 23 fish m^{-2} and 31 decapods m^{-2} . Algae patches were not much more productive, averaging 27 fish m^{-2} and 35 decapods m^{-2} . Standing crops in *Halodule* patches, however, increased considerably to means of 54 fish m^{-2} and 161 decapods m^{-2} . Unless fishes and decapods displaced from mud, algae, and *Halodule* patches are accommodated into *Thalassia* beds and are not lost due to crowding effects, we hypothesize that at any given time the sum of these floral patches plus the remaining healthy *Thalassia* mead-

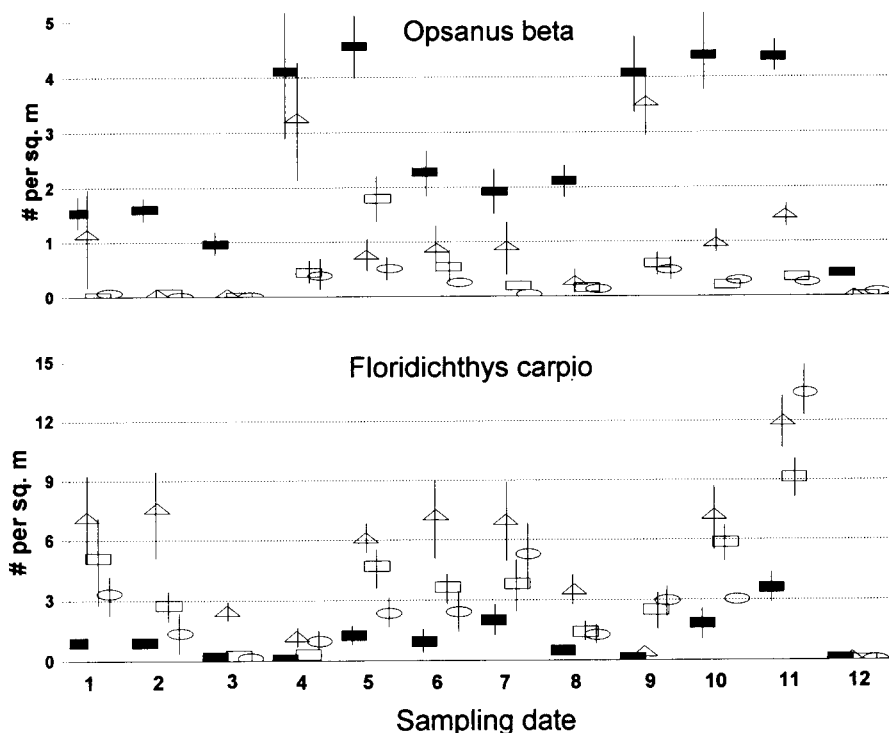


Figure 6. Mean densities of *Opsanus beta* and *Floridichthys carpio* by sampling date and macrophyte type. Closed box = *Thalassia*, open triangle = *Halodule*, open box = algae, open oval = mud. Vertical bar = ± 1 SE (if not visible, SE bar is smaller than symbol height).

ows leads to lower overall standing crops in Florida Bay, opposing the premise of Orth et al. (1984).

Species richness and diversity, however, are enhanced by *Thalassia* mortality. Our results indicate that, on a local scale, increased species richness and diversity were likely to be found in patches atop bank-top seagrasses in any given month. These increases were due primarily to distinct reductions in densities of many fishes and decapods in those patches relative to adjacent *Thalassia*, not necessarily to increases in numbers of species responding to new floral types. Because these patches are ephemeral (*Thalassia* can recolonize a small mud patch in 12-14 mos; Thayer et al., 1994), increases in species richness and diversity are also temporary. However, recolonization is neither rapid nor persistent in all locations. We observed large (100 to 1000 m²) denuded areas on eastern Sandy Key Bank that remained bare from July 1990 to October 1991, and Thayer et al. (1994) noted repeated floral mortality following colonization of specific patches.

Community-level effects of habitat heterogeneity, such as changes in species richness or total abundance and composition of fishes and decapods, depend upon floral species or canopy architecture. In Florida Bay, all of the most common fishes and decapods were found in all floral types but their densities were variable. This may not be the case everywhere. Fish density and diversity in Puerto Rico *Thalassia* and *Syringodium* beds were comparable, but species compositions were distinctive (only eight of 43 fish species were

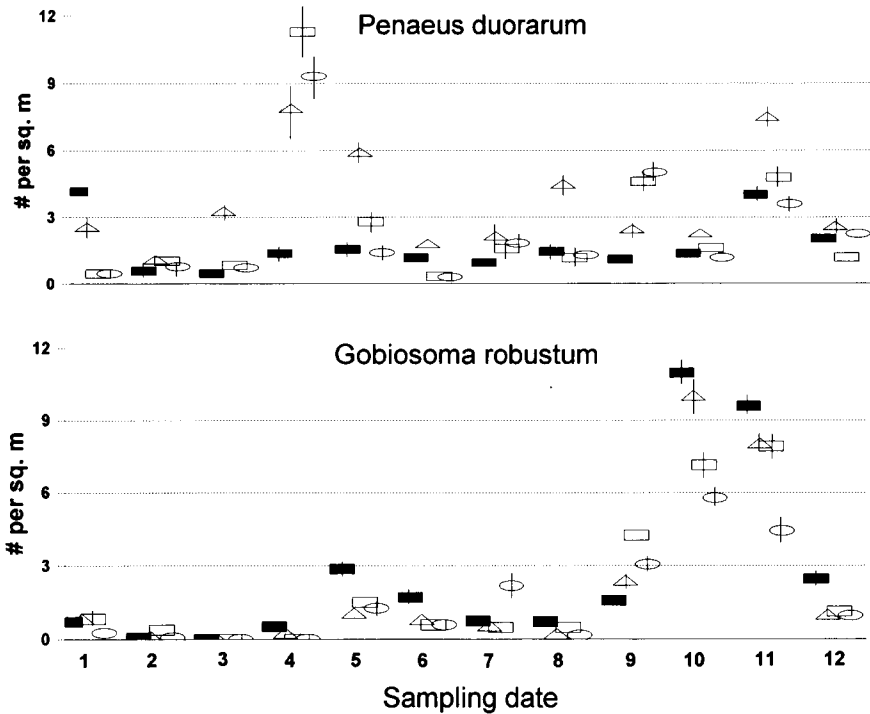


Figure 7. Mean densities of *Penaeus duorarum* and *Gobiosoma robustum* by sampling date and macrophyte type. Closed box = *Thalassia*, open triangle = *Halodule*, open box = algae, open oval = mud. Vertical bar = ± 1 SE (if not visible, SE bar is smaller than symbol height).

found in both habitats; Martin and Cooper, 1981). Fish and decapod densities in the seagrasses *Zostera capricorni* and *Posidonia australis* in New South Wales, Australia, exhibited species-specific increases or decreases due to seagrass structural heterogeneity (Bell and Westoby, 1986a). However, significant differences in densities of fishes and decapods due to small scale heterogeneity within seagrass beds did not translate to the larger scale, i.e., among seagrass beds (Bell and Westoby, 1986b; Worthington et al., 1992).

To examine community stability, we compared our data from daylight sampling on Sandy Key and Dildo Key Banks with those obtained in 1984-85 by Sogard et al. (1987) and Holmquist et al. (1989a, b) at their "Atlantic" and "Gulf" bank-top sites (Table 5). The Atlantic site was a *Thalassia* bed near Buchanan Key, 22 km southeast of Sandy Key Bank, and the Gulf site was predominantly *Halodule* mixed with some *Thalassia* near Oyster Key, 6 km northwest of our site. Although collecting methods differed (1 m² throw trap versus 2.6 m² drop trap), both are considered quantitative gear. All sites were in depths <1 m, and *Thalassia* sites were comparable in terms of seagrass shoot density and aboveground biomass (Table 5). However, our *Halodule* patches exhibited shoot densities nearly 4 times greater and seagrass biomass 85% lower than in the Oyster Key *Halodule* beds. This is most likely due to the young age of our patches versus a permanent *Halodule* meadow. Mean densities of many nekton species inhabiting bank-top *Thalassia* and *Halodule* differed between 1984-85 and 1990-93 (Table 5). Overall fish abundances

Table 5. Mean daytime values for water, floral, and dominant macrofaunal components of two seagrass habitats in western Florida Bay before and during *Thalassia* mortality. Data for 1984-85 are from Sogard et al. (1987) and Holmquist et al. (1989a) for *Thalassia* at Buchanan Key and *Halodule* at Oyster Key, while data for 1990-93 are from this study on Sandy Key and Dildo Key Banks. Seagrass aboveground biomass and shoot density, fishes, and decapods are m⁻².

	<i>Thalassia</i>		<i>Halodule</i>	
	1984-85	1990-93	1984-85	1990-93
Number of samples	216	72	180	72
	<u>Environment</u>			
Depth (cm)	29.0	63.0	48.0	62.0
Temperature (°C)	25.3	28.6	25.2	28.8
Salinity (ppt)	37.4	37.8	35.3	37.6
Seagrass biomass (g dry)	79.5	70.8	36.7	5.2
Seagrass shoot density	1074	907	548	2090
	<u>Fishes</u>			
<i>Gobiosoma robustum</i>	3.3	6.8	1.6	6.1
<i>Floridichthys carpio</i>	2.2	2.5	1.1	12.2
<i>Opsanus beta</i>	1.8	6.8	0.6	2.3
<i>Anarchopterus criniger</i>	1.7	0.2	0.4	< 0.1
<i>Lucania parva</i>	0.7	54.5	1.6	19.0
<i>Hippocampus zosterae</i>	0.4	0.3	1.3	0.4
All fishes	12.1	73.8	8.9	43.0
Number of fish species	33	21	35	20
	<u>Decapopds</u>			
<i>Thor floridanus</i>	108.1	318.7	49.0	75.0
<i>Periclimenes americanus</i>	5.3	0.5	35.3	1.4
<i>Pagurus maclaughlinae</i>	1.5	0.1	8.3	0.9
<i>Hippolyte zostericola</i>	1.1	10.3	22.2	4.5
<i>Alpheus heterochaelis</i>	0.8	0.9	8.4	0.3
<i>Penaeus duorarum</i>	0.8	4.5	9.5	9.4
<i>Latreutes fucorum</i>	0.2	-	4.6	-
<i>Tozeuma carolinense</i>	< 0.1	< 0.1	2.5	0.1
<i>Periclimenes longicaudatus</i>	< 0.1	-	21.9	0.2
All decapods	125.5	338.9	170.6	94.0
Number of decapod species	36	24	34	35

increased in both floral types, as did decapod abundances in *Thalassia*. The most notable increases between sampling periods were for *L. parva* and *T. floridanus* in both seagrass types, while large decreases in abundance were found for *Periclimenes* spp. in *Halodule*. *H. zostericola* densities increased in *Thalassia* but decreased in *Halodule*. In general, more species were collected in 1984-85, but this was likely due to the larger number of samples. This comparison indicates a degree of instability in Florida Bay, but we can not determine whether this was due to *Thalassia* mortality or to other factors such as variations in local rainfall and ensuing salinity patterns.

Our results may have portrayed one stage in the continuing evolution of Florida Bay. More recent comparison of pre- and post-mortality conditions at Oyster Key and Buchanan Key indicated no change in seagrass density and variable responses in densities of fish

and shrimp species between 1984-86 and 1994-95 (Matheson et al., 1995). However, others reported that between decades seagrass and macrofaunal densities continued to decline throughout Johnson Key Basin and that macrofaunal species composition continued to change through reduction of historical dominants and increase in formerly uncommon species such as bay anchovy *Anchoa mitchilli* (Hoss and Thayer, 1995; Robblee, 1995). Synoptic macrofaunal monitoring (1993-95) indicated no bay-wide changes in species composition in reference to historical data, but several basins affected by seagrass mortality were characterized by increased fish diversity following the decline of rainwater killifish (Colvocoresses and McMichael, 1995).

Most of the organisms susceptible to our sampling gear were small resident species and juveniles of transient or pelagic species that are potential prey for larger fishes and invertebrates. Indications from data collected within Everglades National Park are that recreational catch per unit effort of gray snapper, spotted seatrout, red drum *Sciaenops ocellatus*, and common snook *Centropomus undecimalis* in 1995 equalled or exceeded 1980-1990 averages (Schmidt, 1995). Expanding to Monroe County, Florida, no long term declines in landings of mullets (*Mugil* spp.), spotted seatrout, gray snapper, Florida stone crab, or Caribbean spiny lobster *Panulirus argus* have been associated with seagrass mortality (Bohnsack et al., 1994; J. O'Hop, Florida Department of Environmental Protection, pers. comm.), other than those due to declines in fishing trips for aesthetic reasons. Pink shrimp landings from the Tortugas grounds west of Florida Bay experienced a 50% decline in the late 1980s but had recovered by 1994 (Sheridan, 1996). Our data indicate that pink shrimp densities were not generally linked to vegetation type, so pink shrimp were unlikely to be impacted by increased habitat heterogeneity. It is possible that this decline was exacerbated by *Thalassia* mortality and ensuing poor water quality in Florida Bay, but pink shrimp stocks may have been in poor condition for other reasons.

In summary, seagrass mortality has led to increased faunal diversity in the new floral mosaic on Florida Bay bank-tops. These increases were due primarily to distinct reductions in dominant fish and decapod densities when moving from healthy *Thalassia* to mud, algae, and *Halodule* patches, not to increases in numbers of species. No long term declines in landings of commercially and recreationally important fishery organisms have been associated with seagrass mortality, local habitat heterogeneity or changes in composition of the forage base.

ACKNOWLEDGMENTS

This research was funded by NOAA Coastal Ocean Program Grant EHP-64 and by the National Marine Fisheries Service, Southeast Fisheries Science Center, Galveston Laboratory. We would not have completed this work without field and laboratory assistance from E. Klima, D. Emiliani, K. Hammerstrom, K. Torralva, M. Grose, A. Burke, G. Matthews, T. Baumer, M. Van, and S. Humphries (National Marine Fisheries Service at the time of collections); Everglades National Park rangers and support personnel; and M. Robblee (U. S. Geological Survey). Constructive reviews of this manuscript were provided by L. Rozas, M. Robblee, and E. Matheson, and by several anonymous referees.

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DATE ACCEPTED: May 14, 1997.

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